

All-day activity of *Dolichovespula saxonica* (Hymenoptera, Vespidae) colonies in Central Finland

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Abstract

In social vespid wasps, colony activity varies at many temporal scales. We studied the peak season activity (number of individuals entering the nest per min) of colonies of the social vespine wasp *Dolichovespula saxonica* in its native range in boreal Finland. Six colonies were monitored non-stop for a full day, starting before sunrise and ending after sunset. Shorter monitoring was carried out before and/or after the full-day monitoring. All colonies were active before sunrise and after sunset, and the overall activity was positively linked with colony size. Activity showed irregular minute-to-minute cycles in all colonies. The broader within-day dynamics were idiosyncratic among the colonies: activity varied generally between 40–100% of the peak, there were usually a few peaks per day, and the timing of the peaks varied. Ambient temperature was not related to activity dynamics consistently. Our study provides high-resolution information about the all-day activity of *D. saxonica* and underscores high among-colony variability in the dynamics of vespine wasps.

Keywords

Nest activity, social wasps, time series, traffic rate, Vespinae

Introduction

In social vespid wasps, colony or nest activity varies at many temporal scales: within and between days, as well as over seasons. It is well established that the consistent seasonal change in the overall activity of successful colonies is largely related to change in colony size (Kasper 2004; Archer 2012). More intriguing is the within-day variation in

activity, which apparently is linked to environmental conditions (Kasper et al. 2008) and workers' allocation of time to different activities, such as foraging and nest maintenance (Archer 2000a, 2004). Knowledge on colony activity and its variation in different environments are biologically interesting as such, provide fundamental background for other research tasks, and are needed for effective monitoring and management of wasp populations (e.g. in estimating colony size).

Colony activity can be divided in two interrelations: activity inside and outside of the nest. Studies on outside activity generally focus on flight activity, which is measured as traffic rate (i.e. the number of incoming and/or outgoing wasps). Colony-specific traffic rate and its daily variation are influenced by the developmental stage of the colony, ambient environmental conditions and time of day (Kasper et al. 2008; Archer 2012). There are also interspecific differences in overall activity of mature colonies, largely due to differences in colony sizes, but interspecific differences in within-day dynamics are poorly known. The extant studies monitored the within-day activity only for a limited and/or discontinuous time (Gaul 1952a; Potter 1964; Akre et al. 1982; Heinrich 1984; Archer 2000a, 2004; Kasper 2004), and thus were not able to capture the detailed dynamics and provide comprehensive time series analysis. Also, some older studies have studied only one colony, so it has been impossible to conclude anything general about the within-day dynamics.

Most studies on colony activities of Vespinae have focused on *Vespula* (Archer 2012); in fact, we are only aware of two activity studies of *Dolichovespula* (Brian and Brian 1952; Heinrich 1984). Furthermore, vespid activities have been little studied in the boreal region (but see Pallet and Plowright 1979), which differs from temperate and tropical regions in terms of macroclimate and photoperiodism, day length in summer in particular. Because wasp activity is closely linked with the intensity and duration of daylight as well as weather (Gaul 1952a; Potter 1964; Kasper et al. 2008; Kelber et al. 2011), within-day activity of colonies may vary in different regions. Some studies on colony activity have been done with laboratory colonies of *Vespula* (e.g. Gaul 1952a; Potter 1964; Roland and Horel 1976; Vetter and Visscher 1995), which again may lead to false generalisation to natural colonies and to *Dolichovespula*.

In boreal and temperate climates, vespid colonies are annual, each founded by a single queen (Archer 2012). The Saxon wasp, *Dolichovespula saxonica* (F., 1793), is a widespread and abundant species in Finland. It constructs aerial, free-hanging nests, which are often in buildings, cavities or bird nest boxes (Pawlikowski and Pawlikowski 2010; Archer 2012; Nadolski 2012; Broughton et al. 2015). Colonies of *Dolichovespula* (incl. *D. saxonica*) are smaller (a few hundred workers) and colony cycle is shorter than those of *V. vulgaris* (L.) and *V. germanica* F. (Douwes et al. 2012). In Finland, the colony size of *D. saxonica* typically peaks from mid-July to mid-August (Douwes et al. 2012; pers. obs.).

We studied the all-day activity of *D. saxonica* colonies in the native range of the species in boreal Finland at peak season. Flight activity was measured as traffic rate (number of ingoing individuals) with one-minute accuracy, which allowed to examine high-resolution variation in activity. We asked: 1) are the traffic rates and traffic rate dynamics similar or idiosyncratic among colonies; 2) what are the characteristics of

the traffic-rate time series; and 3) does ambient temperature influence within-day dynamics? To understand among-colony variation in traffic rate, nest characteristics and parasitism were recorded.

Methods

Study area and nests

The study was conducted in Jyväskylä, Central Finland, which belongs to the middle boreal zone. The studied wasp nests ($n = 6$) were inside wooden bird nest boxes (1.3–2.0 m above ground; Suppl. material 1: Table S1) in semiurban broadleaved forests, 130 m to 3.5 km from each other. Wasp nests in bird nest boxes were selected, because they were easy to find and monitor, and nest boxes provide similar conditions, thus increasing comparability among nests. During monitoring, ambient temperature (8.8–28.5 °C; Suppl. material 1: Table S1) was between 2 °C and 35 °C, which are the thresholds necessary for foraging of some *Vespula* and *Dolichovespula*, and presumably close to the thresholds for *Dolichovespula saxonica* (Gaul 1952a; Blackith 1958; Potter 1964; Heinrich 1984; pers. obs.).

To allow re-monitoring, the nests were removed, dissected and their characteristics were recorded some weeks after the full-day monitoring (Suppl. material 1: Table S1). Because the nests were close to their peak size during the main monitoring, the measured characteristics represent well the situation during monitoring. Even if this would not be the case, it would only affect the correlation analysis between the nest size and mean traffic rate. The basal comb consisted always of small cells and the last, outermost comb of large cells. Because the in-between combs consisted of mixed large, intermediate and small cells, which were difficult to separate (see also Greene et al. 1976; Archer 2012), we do not provide separate counts of small and large cells. This should not affect our conclusions, because the number of small and large cells correlate in mature successful colonies (Archer 1981). The studied colonies were successful as they produced males and/or queens.

Monitoring

In all nests, we and nine assistants did one non-stop, full-day monitoring close to the peak activity of the season (14 August 2020 in one nest and 14–23 July 2021 in five nests; hereinafter peak season). Peak season was determined based on a few shorter midday monitoring (Suppl. material 1: Fig. S1). Two of these nests were re-monitored for a full day 14 and 15 days later, and one nest for shorter time; we also aimed to re-monitor the other nests but their activity ceased. Each observer monitored the nest continuously for two hours. The full-day monitoring started at ($n = 1$), or before ($n = 7$; med. = 17 minutes, min.–max. = 4–41 minutes), sunrise and continued as long as wasps were active (med. = 55 minutes after sunset; min.–max. = 14–87 minutes); monitoring was done visually with a stopwatch. Colony activity was measured as the

number of individuals returning to the nest per minute (hereinafter traffic rate; see Vetter and Visscher 1995; Archer 2000a; Kasper 2004; see Gaul 1952a for discussion on using uni- vs. bidirectional traffic). During monitoring typical weather varied from half cloudy to sunny, was rainless, and the wind force at the ground level was calm to moderate breeze. In one nest (Sippula), there were 20 minutes of drizzle rain and a few stronger breezes during monitoring. Ambient temperature was recorded a few meters from the nests, 0.5–1.5 meters above the ground every half an hour, using a digital thermometer (model 210 by Suomen lämpömittarit Oy; measuring accuracy 0.1 °C) that was in the same place all day.

Statistics

Traffic rates were expressed and analysed as individuals per minute, except in figures where longer time periods were needed for illustrative reasons. For example, within-day activity was illustrated using centered moving averages, calculated over seven 5-min periods (i.e. 35 min). Odd number of 5-min periods was used for illustrative reasons, and the 35-min moving average was used because it adequately smoothed the data and revealed underlying trends. The average full-day traffic rates were calculated between sunrise and sunset. Coefficient of Variation (**CV**) and autocorrelation analysis were used to describe variation in traffic rates. There were only 12 minutes of missing data, which were replaced with the data immediately before the gap. Linear regression was used to analyse the relationship between the mean traffic rate and colony size, and between the mean traffic rate and its variation (CV).

To identify patterns in the sequence of traffic rates over time, we used an autocorrelation analysis. First, sequence plots and the augmented Dickey-Fuller Test (**ADF**), as well as autocorrelation and partial autocorrelation plots (with a maximum number of lags = 30) were used to detect trends and seasonal effects in the time series. For subsequent autocorrelation analyses trends were removed by transforming the data using differencing ($d = 1$), i.e. making the time series stationary. Transformation was needed to analyse patterns in the fine-scale, minute-to-minute variation in traffic rates.

To analyse the relationship between temperature and within-day traffic rate dynamics (i.e. the broad variation in the mean traffic rate over day), we used the Expert Modeler option in SPSS, which automatically identifies and estimates the best-fitting ARIMA or exponential smoothing models; only non-seasonal models were considered. Because temperature was measured at 30-min intervals, we made it continuous by replacing missing values using linear interpolation. In the Expert Modeler, the final model only includes those independent variables, which have a significant relationship with the dependent series. Model fit was judged by the non-significance of the Ljung-Box statistic and visual judgement of the residual autocorrelation plots; in Sippula, the non-significance was reached after automatic removal of outliers. No transformations were used.

All analyses were conducted with IBM Statistics SPSS 26.0, except the augmented Dickey-Fuller Test which was conducted with RStudio Version 1.3.1093 (library 'tseries').

Results

During the peak season, *D. saxonica* flight activity started about half an hour before sunrise and increased sharply, whereas the evening decline was more variable (from sharp to gradual) and ended 28–77 minutes after sunset (Figs 1–8). Overall, *D. saxonica* colonies made an average of 3958 (1074–9140) trips per nest and day. The mean sunrise-to-sunset traffic rate among nests varied from 1.1 to 7.2 wasps per minute (Table 1). The number of combs varied from 3 to 7, and the total number of cells from 525 to 1784. Traffic rate was positively related to the total number of cells and combs (linear regression: $r = 0.97$, $r^2 = 0.95$, $p = 0.001$, and $r = 0.89$, $r^2 = 0.79$, $p = 0.018$, respectively, $n = 6$), but not to the number of cells in the basal comb ($r = 0.50$, $r^2 = 0.25$, $p = 0.32$).

Table 1. Traffic rates (number of individuals entering per minute) for the studied *Dolichovespula saxonica* colonies in Central Finland from sunrise to sunset, and colony size.

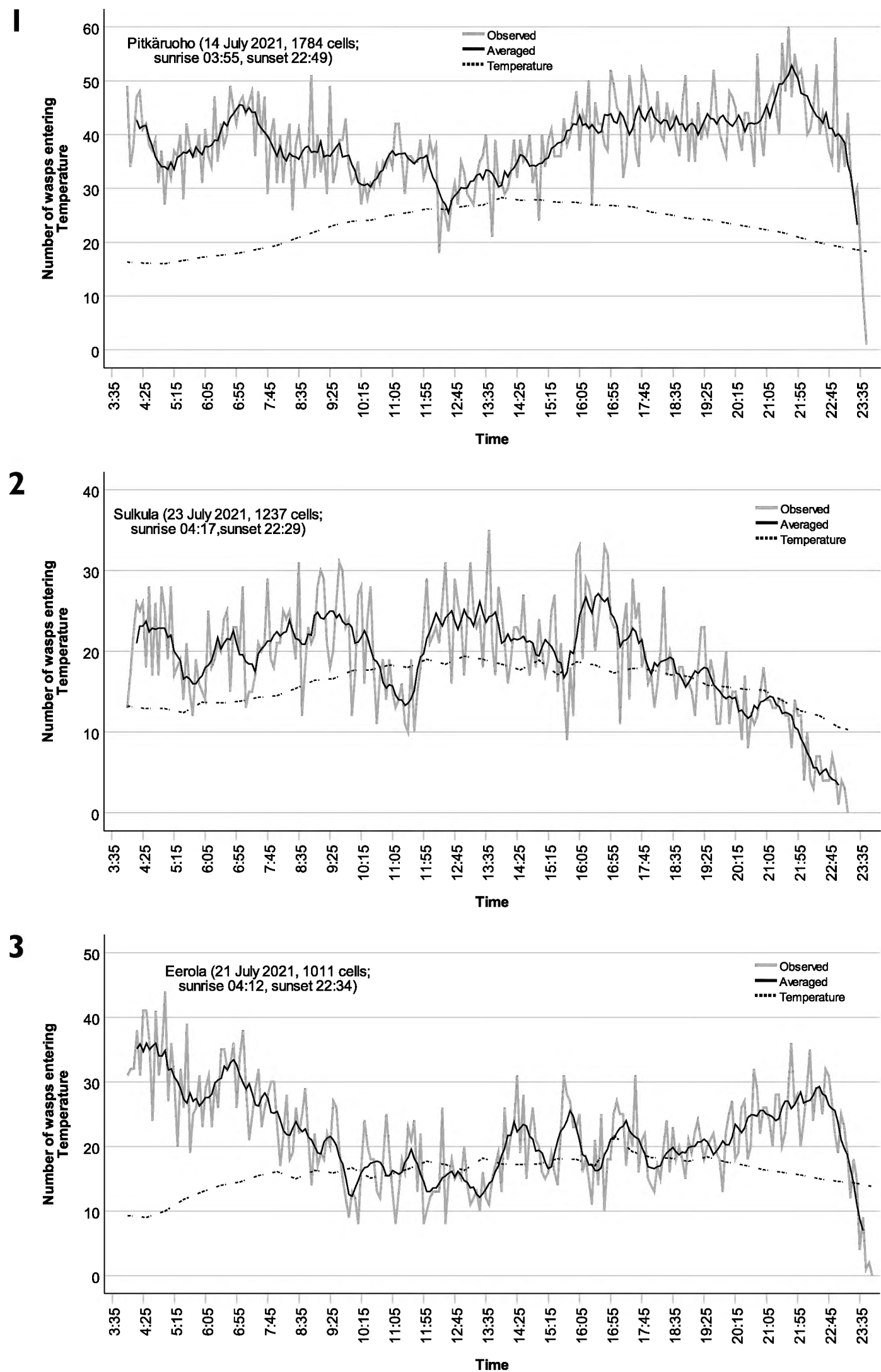
Colony	Med.	Mean	SD	CV%	Min	Max	Sum [†]	# of combs	# of cells
Pitkäröho	8.0	7.76	2.80	36	0	22	8789	7	1784 [‡]
Sulkula	4.0	3.91	2.16	55	0	12	4279	5	1237
Eerola	4.0	4.41	2.34	53	0	16	4859	4	1011
Sippula	2.0	2.18	1.63	75	0	13	2396	3	662
Haukanniemi	1.0	1.07	1.08	101	0	6	1037	4	585
Siirtola	1.0	1.28	1.10	87	0	5	1439	3	525 [‡]
Sulkula re-measured	1.0	1.44	1.29	90	0	9	1456		
Eerola re-measured	1.0	1.55	1.53	98	0	10	1585		

[†]Total number of trips from sunrise to sunset; [‡]Estimated, see Suppl. material 1: Table S1.

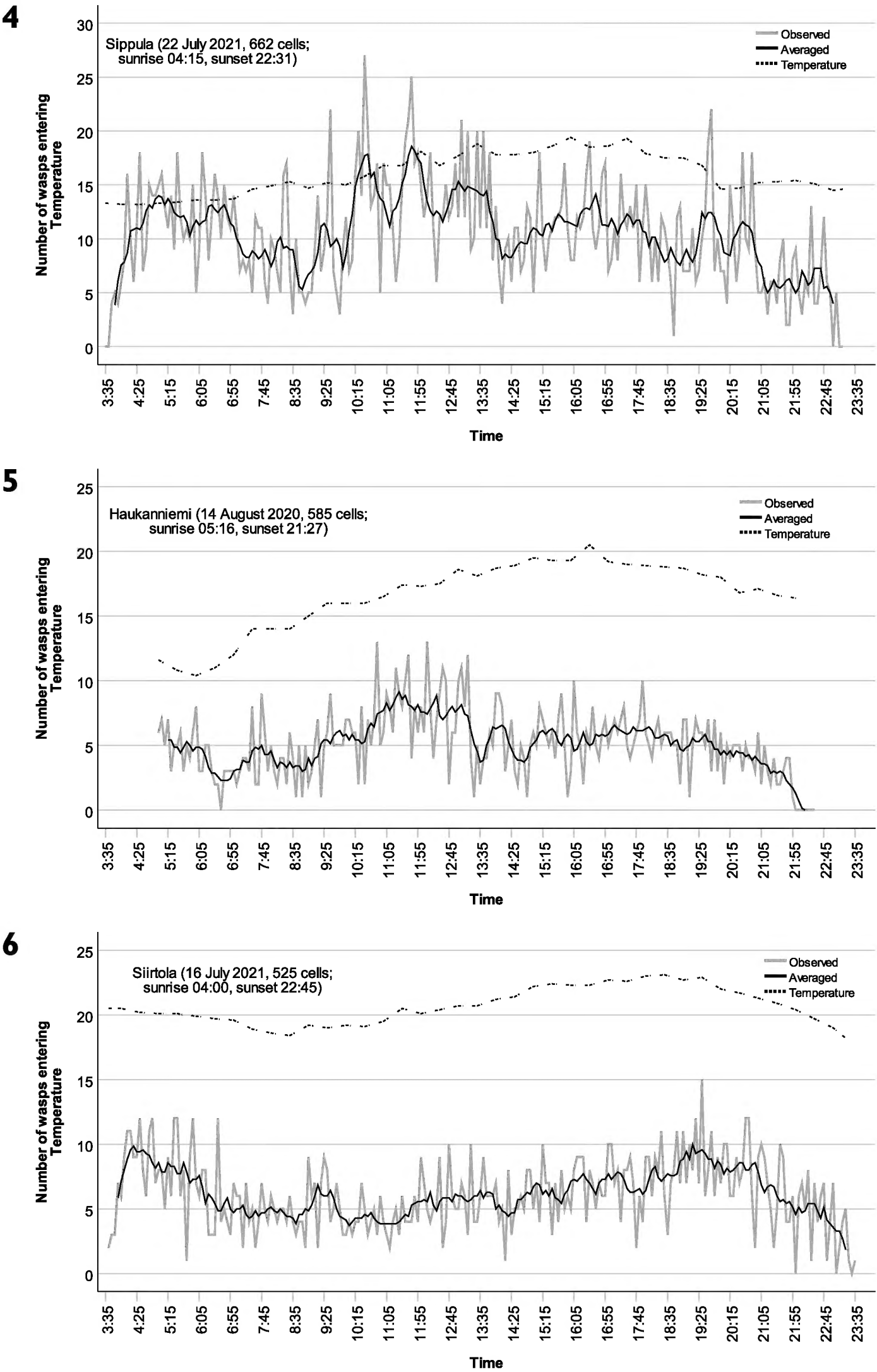
The overall level of variation in the 35-minute traffic rate differed among nests (CV% min-max = 36–101; Table 1), and the higher the mean daily traffic rate, the lower the CV% (linear regression: $r = 0.94$, $r^2 = 0.89$, $n = 8$, $p < 0.001$). In all nests, the traffic rate was non-stationary, i.e. the mean varied during the day (Figs 1–8). Visual judgement of non-stationarity was supported by the ADF-test in all nests (ADF > -3.06 , $p > 0.11$, lag order = 30; ADF = -3.40 , $p = 0.054$, lag order = 45 in Sippula).

The number and timing of the peaks and lows varied among nests, and the lows of the 35-min moving average were generally about 40% of the peak (Figs 1–8). This broad variation in the mean within-day traffic rate was related to the ambient temperature only in Eerola and Siirtola but in opposite direction (Figs 1–8; Suppl. material 1: Table S2). There was also irregular cyclicity in minute-to-minute traffic rates (ACF = -0.52 to -0.46 , $p < 0.05$ at lag = 1; Suppl. material 1: Figs S2, S3).

Parasitism rate was low. No parasitoids or parasites were found in two nests. Eight cocoons of *Sphecophaga vesparum* (Curtis) (Hymenoptera: Ichneumonidae) were found in one nest, which is only 0.8% of the total number of cells. Larvae of *Aphomia sociella* (Linnaeus) (Lepidoptera: Pyralidae) were found in three nests (2, 25 and 94 individuals). (Suppl. material 1: Table S1.)

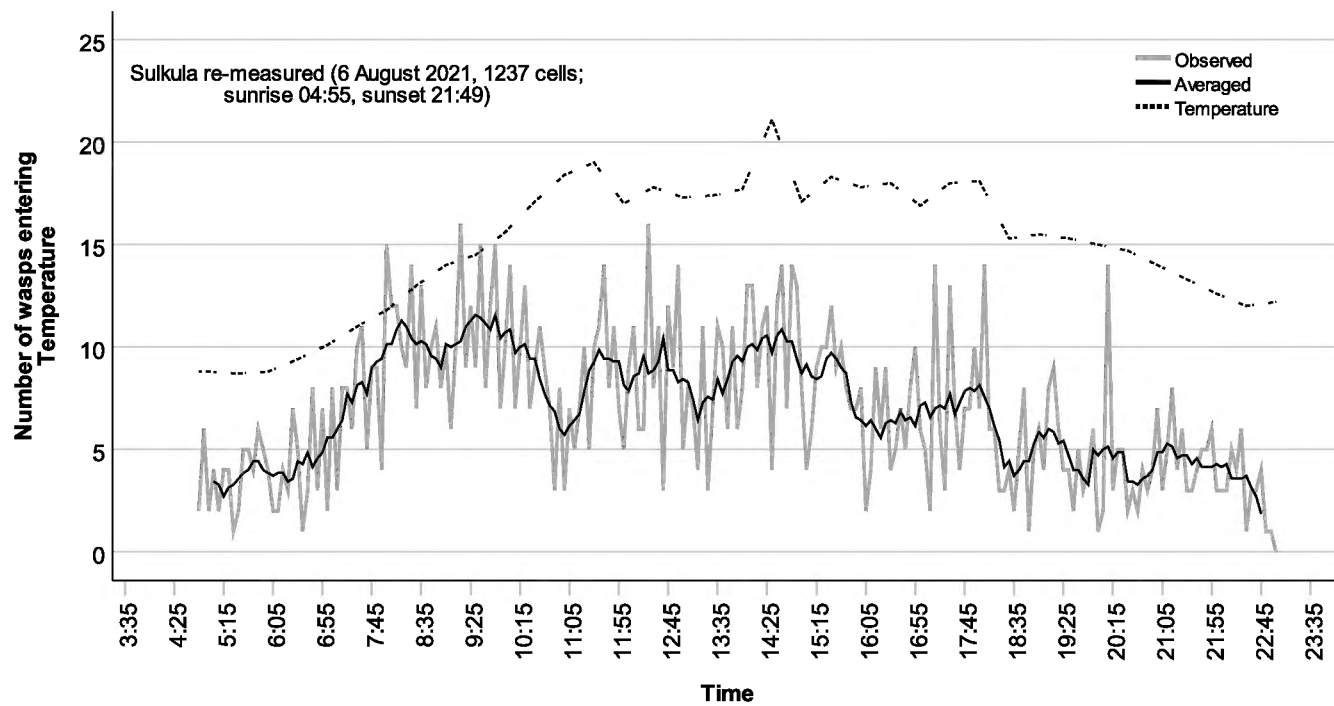


Figures 1–8. Observed number of *Dolichovespula saxonica* individuals entering the nest per 5 min, the 35-min centered moving average, and ambient temperature (°C).

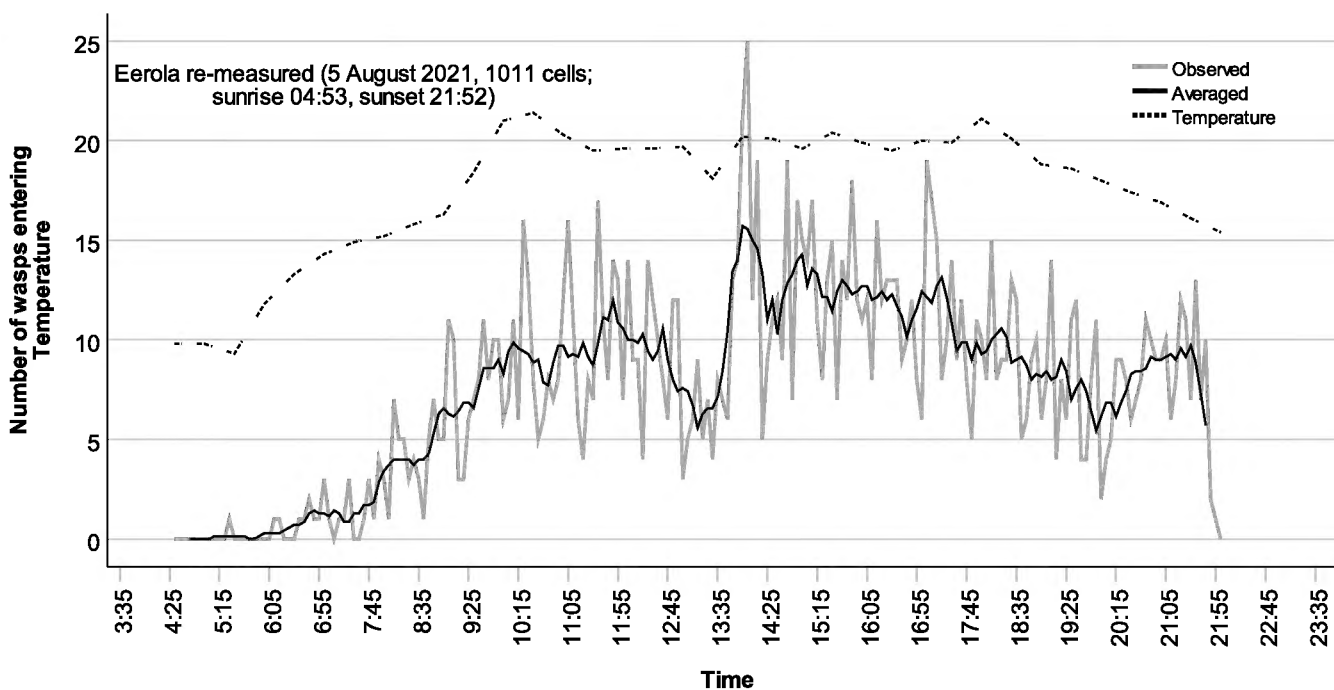


Figures 1–8. Continued.

7



8



Figures 1–8. Continued.

The mean daily traffic rate as well as traffic rate dynamics changed over season. Those two nests, which were re-monitored for a full day later in the season, had then a lower traffic rate, different timing of peaks and showed a more gradual increase (over 2 to 3 hours) after sunrise; the evening decline was inconsistent among the two nests. Furthermore, the timing of the mid-day activity peaks varied over the season, but subtly (Suppl. material 1: Fig. S4).

Discussion

Our results support the long daily activity of vespine wasps (Gaul 1952a; Archer 2004; Kasper et al. 2008 for *Vespula*; Brian and Brian 1952 and Heinrich 1984 for *Dolichovespula*). Because we generally started the monitoring at sunrise or slightly

before, after the flight had already started, it is apparent that the flight starts about half an hour before sunrise and increases rapidly. In the most extreme case, the flight continued over an hour after sunset, which is likely related to long dusk in northern latitudes. Thus, in boreal Central Finland, *D. saxonica* is active about 20 hours in July and a few hours less in August. Our results indicate that the length of the daily activity of *D. saxonica* is linked with the duration and amount of daylight, similar to *Vespula* (Gaul 1952a; Potter 1964; Kasper et al. 2008; Kelber et al. 2011). In addition to the shortening of the daily activity period after the peak season, also the dynamics change: the timing of the daily peaks was different and the increase in the morning activity became more gradual. With only two nests re-monitored for a full day, our conclusions concerning seasonal changes in the within-day activity patterns of *D. saxonica* are preliminary but do support the idea of high variability.

The sunrise to sunset traffic rates varied among nests and reflected colony sizes. Daily traffic rate is a function of worker numbers and flight activity. Worker numbers are largely related to seasonal phase of a colony, but other intrinsic and local environmental factors have a role since nearby, mature colonies vary in size (Nadolski 2012; this study). The positive relationship between traffic rate and total number of cells was much stronger and less variable than documented for invasive *V. germanica* (cf. Kasper 2004). Due to the high within-day variability in activity, traffic rate can only be used as a rough indicator of colony size in *D. saxonica* and should be estimated at least over half an hour (cf. Malham et al. 1991). The within-day variation of colony's traffic rate reflects differences in flight activity, which may be related to workers allocation of time to different activities (Archer 2000a) or variation in weather (Kasper et al. 2008). The full-day monitoring was carried out at, or near the peak activity during favourable weather (see below), we therefore assume that most trips were foraging trips and the time devoted to nest enlargement was minimal. Parasitism was unlikely to have a great effect on traffic rates (see below). As the ceased nests were removed some weeks after the main monitoring, it is possible, yet unlikely given the developmental times of *Dolichovespula* (Archer 2000b; Archer 2012), that the measured nest characteristics did not closely reflect the characteristics during monitoring.

At the peak season, *D. saxonica* activity dynamics were idiosyncratic among nests, i.e. the timing of the activity peaks, based on a 35-min moving average, varied among nests. The morning peak, which was generally not the daily peak, was followed by a variable period of lower traffic rate. The only extant study of the within-day dynamics of *Dolichovespula* (one nest of *D. maculata*) indicated early morning and late evening peaks (Heinrich 1984). Similarly, the typical daily activity of *Vespula* has often been characterised as having a sharp peak in the early morning and late evening (Spradbery 1973; Edwards 1980); yet, the more recent studies indicate high variability in the timing of the peaks (Potter 1964; Edwards 1980; Heinrich 1984; Archer 2004; Kasper 2004). Latitudinal variation in the sharpness of the morning and evening activity peaks might be related to the latitudinal variation in the length of dawn and dusk. Because we did not re-monitor the colonies during the peak season, we cannot conclude about the day-to-day variation in the dynamics of a single nest during peak

season. Yet, our study shows that there are no consistent species-specific dynamics in *D. saxonica* colonies. To disentangle the effects of colony-specific characteristics (behaviour, parasitism, nest site, environment) and daily weather on dynamics requires another study.

Traffic rate varied also at finer resolution and showed irregular cycles of a few minutes. The only study on the trip or inter-trip times of *Dolichovespula* (Brian and Brian 1952) showed rather constant times spend in the nest, even for individuals carrying out different activities (fluid, pulp or flesh collecting), whereas the times spend outside were more variable for the activities. In general, constancy in the times of in-nest or outside activities can promote regularity in cycles. Our observations about the cycle length are also in line with the mean trip times for below-ground *V. vulgaris* (Archer 2012); the in-colony time of *D. saxonica* is likely to be shorter than that of the below-ground *V. vulgaris*, because there is no need for earth removal. Cyclicity and cycle length were not conditional on a particular nest, which might be the case if availability and distribution of food were the underlying causal factors. Yet, there is evidence that wasps tend to revisit good foraging sites and might be capable of information sharing (Santoro et al. 2015) or local enhancement (D’Adamo et al. 2000) regarding food sources, which could maintain similar trip times and hence rough cyclicity in activities. Furthermore, to decrease predation risk, wasps are likely to coordinate their activities so that the nest is never left unattended.

Flight activity of wasps is affected by weather, particularly extreme temperature, rain, wind and light conditions (Gaul 1952b; Potter 1964; Kasper et al. 2008; Archer 2012). Because we monitored the activity on days when the wind was generally calm to moderate, the sky clear or half cloudy, and rainfall negligible, it is likely that these had an irrelevant effect on overall activity or activity dynamics. Temperature, in turn, might have had a larger, yet temporally inconsistent effect. Ambient temperature outside the nests was always between the lower and upper thresholds for flight activity (see Blackith 1958; Potter 1964; Heinrich 1984; Coelho and Ross 1996; Kasper et al. 2008) and remained rather stable during mid-day; thus, it neither explains the cyclicity at the scale of minutes, nor the irregular variation in mean traffic rate during the day (the statistically significant relationships between traffic rate and temperature in two colonies were in opposite directions). However, June and July 2021 were record-warm in Central Finland, and temperatures over 30 °C in the direct sunlight were regularly observed. Most of the studied nests experienced direct sunlight for some, but different time during the day, so it is possible that the in-nest temperature raised over the regulated 28–31 °C (see Heinrich 1984). This might have affected differently the within-day flight dynamics among the nests and it could explain the variation in mean traffic rate at the scale of half an hour to some hours. Indeed, a few times a buzzing sound was heard and ventilating workers were seen at the nest entrance suggesting fanning behaviour to cool the nest (see Potter 1964; Heinrich 1984). The consequences of extreme in-nest temperatures are not clear. On the one hand, fanning might decrease traffic rates, but on the other hand, high temperatures can shorten feeding times, as observed for *Vespula* (Jandt et al.

2010), and thus increase traffic rates. Because similar variation in traffic rates has been observed for under-ground colonies of *Vespula* (Kasper et al. 2008; Archer 2012; pers. obs.), which are likely to maintain more stable temperature than exposed *Dolichovespula* nests, the variation in traffic rate remains a mystery. To better resolve the effect of temperature on activity, future studies should preferably measure in-nest temperatures.

Parasitism can affect colony size and hence overall colony activity, but unlikely affect within-day dynamics. In the studied colonies, parasitism rate by *S. vesparum* and *A. sociella* was low, so the effect of parasitism on any of the measured parameters is negligible. Low parasitism rate corroborates previous observations (see Archer 2012). Furthermore, because the nests were removed 21, 17 and 19 days after the first monitoring, it is likely that the *A. sociella* infestations occurred near or after the first monitoring, and thus had little effect on traffic rates. Furthermore, *A. sociella* infested colonies can show normal development, especially if infestations occur late in colony development (Archer 2012). Only the traffic rate in the Siirtola nest (94 *A. sociella* larvae) might have been affected by parasitism, since the full-day monitoring was done after the peak activity; yet, the traffic rate was only slightly lower than at the peak and similar to the other colonies of similar size.

Conclusions

Our study provides high-resolution information about the all-day activity of *D. saxonica* colonies. Despite the previous suggestions that vespids, or at least *Vespula*, colonies would have roughly consistent within-day dynamics, the observed idiosyncratic within-day activity among colonies challenges this idea. Together with the recent studies on *Vespula* our results suggest that the within-day dynamics of vespines as a whole are explained mainly in terms of environmental conditions rather than by any innate pattern of changes in colony needs. Furthermore, all colonies showed irregular cycles over a few minutes. This suggests that the trip and inter-trip times are roughly similar in colonies with different environmental surroundings. Future studies should verify the observed patterns in other *Dolichovespula* wasps and, even though laborious, they should combine high-resolution monitoring of colony activity with individually tagged wasps and carefully measured in-nest conditions.

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Supplementary material I

Tables S1, S2, Figures S1–S4

Authors: Atte Komonen, Jyrki Torniainen

Data type: Tables and figures (docx. file)

Explanation note: Nest characteristics, seasonal activity, time series model summary, minute-to-minute dynamics and correlograms.

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